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THE ENDOCRANIUM AND MAXILLARY SUSPENSORIUM OF THE BEE.[1]

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THE chitinous wall which covers an insect's body and lines its interior, is soft and thin for hinges and other pliable parts, and is hardened in places where rigidity is required. It is furthermore folded outwards or inwards into processes which impart additional strength or protection, or for attachment of muscles. The outgoing folds are seen in the pleura of a lobster (allied to insects) and the wing of a bee, and are always double by nature (including the outgoing and returning plates) with interposed nutritive matter, like the meat in a sandwich.

The outgoing plates (or exodemes) have their counterparts in the internal processes (or endodemes), which usually mark the boundaries between adjacent segments of the body, and which are more or less hardened in particular parts, thus forming an endoskeleton. This internal skeleton is most completely developed in the ventral part of the thorax, and where it forms the endocranium, or internal buttresses of the skull. (It may be observed that the insect has also hard processes of the pharynx and stomach which may be collectively termed its splachnodemes.)

Anatomists have not paid much attention to this class of structures, and some eminent students of insect embryology are as silent regarding the endoskeleton as if they had never heard of

[1] Paper read before the Biological Section of the American Association for the Advancement of Science, Boston, Aug., 1880.

such parts. The few references to them already published, are not distinguished by accuracy. Yet it is patent that all efforts to evolve an insect's embryology, or to give the rationale of its head, ought to include as a preliminary study the structure of its internal economy. In our present essay it is proposed to examine these parts in the honey-bee, and to compare them with their representatives in a few other insects.

The upper part of a bee's cranium consists of three parts, epicranium (Fig. 1, EC), clypeus (C) and labrum (LR). The epicranium is the crown, extending from the occipital foramen at back of the head, right over the vertex, to a transverse suture in front of the insertion of the antennæ (AT). It covers the entire roof and back of the head, and is medially divided in many insects (especially in larvæ) into right and left sections. It is flanked on both sides by the large compound eyes (OC), and is continuous with the cheeks which form the sides of the skull in front of the eyes (G).

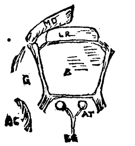


FIG. 1.—Internal view of vertex of bee's skull. EC, epicranium; AT, position of antennæ; C, clypeus; LR, labrum; MD, mandible; G, gena, or cheek; OC, ocular or compound eye.

A remarkable feature of the epicranial region is that it has no endodemes, no such ridges or infoldings as to hold out any suggestion of a tendency to segmentation. It has a few ridges near the occipital foramen, and a rim around the eyes and sometimes about the root of the antennæ; but we have found no trace of latent segmentation in this region. This goes against the doctrine that the antennæ represent a segment in the head; and recent discoveries in embryology indicate the same conclusion.[1]

The clypeus, or "face," is the roof of the mouth cavity. At its lateral borders it affords insertion to the mandibular condyles. (In the Doryphora, or potato-beetle, it is curiously turned in with sockets at its angles for the mandibles.) It also shows such involutions as to bring it into close relations with the endocranial system. Its posterior border (that next the epicranium) bends down into a hard transverse ridge, with thick outgrowths at the postero-lateral angles. From these outgrowths descend two pil-

[1] Balfour denies to the procephalic region any correspondence with somites of the body, and says that "the antennæ can hardly be considered to have the same morphological value as the succeeding appendages." (Comparative Embryology, Vol. I, p. 337.)

lars obliquely downward through the cranial cavity (Fig. 2, MC). These mesocephalic pillars are inserted in the floor of the skull just at the sides of the occipital foramen (FO).

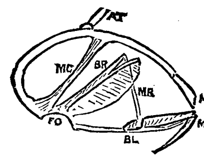


FIG. 2.—Lateral view of bee's skull. FO, occipital foramen; MC, mesocephalic pillars; AT, root of antennæ; BR, basi-suspensorium; MR, medi-suspensorium; BL, basi-labium; MX, maxilla; MD, mandible.

Thus the endocranium consists of a pair of pillars, arising by strong roots from the cranial floor, and fixed above to the clypeus. (The clypeus has to support the mandibles and to afford attachment to many muscles.) Near the top each pillar is forked transversely so as to afford more extensive support. (Fig. 3, MC.)

It is these pillars which render a bee's head so strong, though its shell is rather thin. The mesocephalic pillars of an ant's skull are similar to those of the bee; and we observed short tendons in the neck serving to antagonize them.

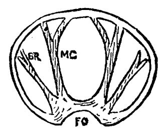


FIG. 3.—Diagrammatic view of bee's skull in transverse section. References as in Fig. 2.

The pillars ascend in front of the cerebral brain-lobes, running between them and the ophthalmic lobes, and keep the large ocular apparatus in its proper place.

Burmeister's well-known account of the endocranium of insects has many errors. He represents that of Hymenoptera as rising from the base and ending in two points; he seems to have broken off the pillars and so missed their attachment to the clypeus. He says that Diptera and Hemiptera have no endocranium. This is partially true of the Muscidæ; but we have shown[1] that in all probability the basal part of the proboscis of these insects represents the endocranium, and there is a rudiment of the endocranial roots in a small bridge across the occipital foramen. In the large gadfly (*Tabanus atratus*), and in the mosquito, we find cephalic pillars as in the bee (besides what seems to be a splachnodeme or pharynx-case supporting the complex oral armature.) *Coreus*, of Hemiptera, though seemingly devoid of mandibles, maxillæ, labium and all processes related to them, has a pair of processes depending from the clypeus, in the position of the upper part of the mesocephalic pillars. These probably support the pharynx and the roots of the long piercing bristles.

[1] See AMERICAN NATURALIST, March, 1880. "On the Proboscis of the House-fly."

Burmeister attributes to Lepidoptera nothing more than a small bar across the occipital foramen. But we find (in the swallow tail, *Papilio turnus)* a strong sub-quadrate frame arising in front of this foramen, and reaching forward so as to be fixed near the roots of the proboscis.

That the mesocranial pillars represent involutions of the outer walls, may be understood from the trunk of the cray-fish, where (as Mr. Huxley has well shown) the ingrowths become plates or ridges, or even pillars. But we find a closer illustration in the heads of some other insects. Cicada has similar pillars with the bee, somewhat flattened out and attached to the sides of the head (the eyes here not reaching so far forward). This would indicate that in the bee the ridges have been displaced inwards by the encroaching of the eyes. (The clypeus of Cicada is transversely barred so as to show about ten pseudo-somites. It is easy to examine these parts from one of its exuviated shells.)

The dragon-fly has a stout ridge below the occipital foramen, sending up processes to the clypeal region, as in the bee. But these processes are broadened out and transparent, and not rigid. The clypeus itself is soft and swollen, and has a deep transverse ridge to meet the processes. Thus the large, weak cranial wall is somewhat but slightly strengthened.

The attempt to correlate the parts of the bee's head with those of the head of the cockroach, gave rise to some interesting revelations. Here Huxley's excellent description of the cockroach ("Anatomy of the Invertebrated Animals") was in good season, but we soon found that his work was superficial and faulty on this part. He states that the endocranium of the cockroach "extends as a cruciform partition from the inner face of the lateral walls of the cranium to the sides of the occipital foramen;" and speaks of the center of the cross as being "pierced by a rounded aperture through which the œsophageal nerve-collars pass." In fact, it is not cruciate in form, but consists of two pillars as in the bee (only softer), and united by membrane some way up, *i. e.*, crotch-webbed like the webbed fingers of a water-fowl. The upper band running across is a fascia binding the two mandibles together (present in the bee, though not thus united with the mesocephalic rods). Thus we have a "tentorium," or mesocephalic plate, forming a thin diaphragm across the middle of the cranial cavity, with thickened borders in front and laterally, and itself concave up-

wards so as to form a channel for the pharynx (Fig. 6, EC). Its perforation is not as in the axis of a cross, but forwards, as if the webbing had ceased at this part. Its correspondence with the parts already described in other insects is easily shown. In the locust the lateral pillars approach more closely, so as to resemble the letter X, but the foramen and other parts are much as in the cockroach.

The Coleoptera appear to want this system. But in following out the relations of the parts I came to a view which, if correct, would explain the anomaly, and which I shall reserve for a later part of this paper.

B. Maxillary suspensorium.—It is convenient to examine together the proximal adjustments of both maxillæ and labium (or first and second maxillæ, as they may be called). These are intimately connected in their mode of attachment in all insects possessed of such parts. In the case of the bee they are strung upon a long framework with elbows and hinges, which is able to thrust them out and to draw them in. Of this framework, which we shall call the "maxillary suspensorium," we have not been able to find any satisfactory description or figure. Schmarda's Zoölogy gives a correct figure of its distal part; but neither Schmarda nor Westwood nor Réaumur appears to have traced the structure to its origin. The prize work on the "Anatomy and Physiology of the Bee," by M. Girdwoyn, published by Rothschild, of Paris, is grossly inaccurate at this part. We shall begin its description from its base, where it is inserted close to the inferior insertion of the mesocephalic pillars, immediately in front of the foramen magnum.

At this point there are, below the mesocephalic pillars, two basi-cranial rods, running forwards towards the oral opening (slightly ascending forwards when the mouth parts are retracted, but nearly horizontal when they are protruded). These basi-cranial rods arise similarly with the mesocephalic pillars; but they are united to the sides of an excavated opening in the basis cranii by a thin web, just as the mesocephalic pillars are joined to the side-wall in Cicada. They are not hinged at their root, but are firmly fixed and widen out here, and are slightly pliant, whilst their motion is limited by the web which binds them to the basi-cranial wall (Fig. 5, BR). (An engineering friend to whom we showed this structure, informed us that it involves the

principle of a machine recently patented for producing a slight and steady motion combined with strength.) The two parallel basi-cranial rods are also connected with each other by a very thin and pliable sheet of chitine, which forms the lower bounding wall of the head at the excavated part, and yet allows perfect freedom of motion to the suspensorial mechanism.

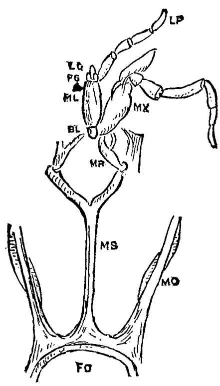
The basi-cranial rods are forked at their distal ends, where they support the *maxillary rami*, one at each side (Fig. 5, MR), which are joined to them by a very perfect elbow-joint, enabling the rami to fold downwards. The rami support the maxillæ, which can thus be protruded or withdrawn. We think that each of these rami corresponds with the cardo or basal segment of the maxillæ of the cockroach or beetle (though this name has been given to the process next to be described).[1]

The *modus operandi* of the maxillæ on these rami is noteworthy. Each maxilla consists of a flat base (stipe), surmounted by a lacinia resembling a knife blade, and bearing a rudimentary palp at the middle; and its lacinia can bend downwards and backwards so as to be out of the way and to present the stipe as a flat projecting plate. When the mouth parts are retracted, the two maxillæ are thus bent down, and their plate-like stipes are approximated, so as to form a hard under lip for the mouth, upon which the mandibles play in their operations (as on a piece of cork, or in cell-making as when the carpenter-bee is operating on wood). The basi and medi-labium then fill the excavated part of the basi-cranial surface. When the suspensorium is being protruded, the thin membrane which borders its proximal joints and which is extended so as to reach the blades of the maxillæ, becomes tense and divaricates them so as to secure their steadiness of motion and to give free play to the intervening labium.

From the distal end of the maxillary rami proceed two *labial rami* to support the labium, thus giving an additional joint, with a hinge which moves freely backward and forward. (This is the piece usually called cardo; we shall call it *labial ramus* of the suspensorium, or labi-suspensorium.) By means of it a very

[1] Dr. Hagen has shown us Wolff's article on "Das Riechorgan der Biene" in *Nova Acta Leop. Carol.*, Band XXXVIII (1875), with beautiful and accurate drawings of the structure of the bee's head. The author does not appear to have studied the parts in the relations here discussed; and he is altogether fanciful in identifying the hard parts and the muscles of the bee's skull with the bones and muscles of the mammalian head.

great degree of motion backwards and forwards is allowed to the labium, which mobility is still further increased by the protrusibility of its ligule or distal piece. The labium consists of a basal piece, usually termed submentum (we would rather call it basi-labium, Fig. 5, BL); of a medial piece, usually termed mentum



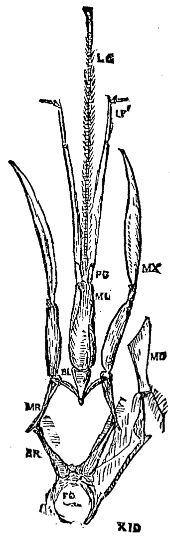


FIG. 4.—Suspensorium and mouth parts of ant. MS, basi-suspensorium; MC, mesocephalic pillar. The other references are as in Fig. 5.

FIG. 5.—Suspensorium and mouth parts of bee. FO, occipital foramen; BR, basi-suspensorium; MR, medi-suspensorium; *below* BL, labi-suspensorium; *to left of* BL, basi-labium; ML, medi-labium; PG, paraglossæ; LP, labial palp; LG, ligule or outer tongue; MD, mandible; MX, maxilla: the terminal part of the maxilla is the lacinia, the basal part is the stipe, its narrow middle part has a rudimentary maxillary palp. One of the endocranial pillars is seen extending from beside the occipital foramen to near the insertion of the mandible.

(we would call it medi-labium, ML), and of what we may call a disti-labium, consisting of paraglossæ (PG), of well-developed labial palps (LP), and of the terminal ligule (LG), about which a great deal has been written.

In such bee-like insects as do not protrude their maxillæ, these parts are more or less simplified, so as often to illustrate and explain the complex arrangement of the bee. Very often the distal parts of the labium are reduced or condensed (so as to resemble somewhat the swollen tip of a housefly's proboscis). In *Stizus grandis*, with non-retractile proboscis, we found the basi-cranial rods to be merely a high ledge running forwards around the excavated part of the basi-cranium, and serving for insertion

of the maxillæ. This shows clearly how the excavation and the rods and connecting sheets arise by an involution of the cranial wall, with thickenings in special tracts.

The large black ant *(Formica pennsylvanica)* carries our thoughts still further. It has only one basi-cranial rod (Fig. 4, MS), extending forward above the basi-cranial wall (which is not excavated). This is derivable from the case of the bee, on the supposition that the basal rods and the margins of the basi-cranial involution have approximated medially so as to coalesce. The ant's suspensorium has a medi-suspensorial pair of maxillary rami (MR), as in the bee; but its labial rami are so small as to be nearly obsolete. Its basi-labium (BL) and its medi-labial case (ML) are much as in the bee; but its disti-labial parts are condensed.

The series of gradations thus attained holds out inducements to pursue the subject, and we may perhaps see the beginning of a new line of discovery in this field. Compare, for example, the maxillary adjustments of the cockroach with those of the insects already described. Here again Mr. Huxley is less happy than usual in his anatomical descriptions. He states that the basal piece or cardo of the maxilla of the cockroach is connected with a thin band which runs round the posterior margin of the epicranium and is firmly united with it only on its dorsal side. He does not indeed represent the maxillæ as directly inserted in the back of the skull, but he regards them as attached to a band which is itself attached to the back or dorsal aspect of the skull, and which he is thus compelled to consider a portion of its exoskeleton. This view, if sustained, would clash with the mode of suspension in the bee, where the maxillæ have been found to have endocranial connections with the base or ventral side of the skull.

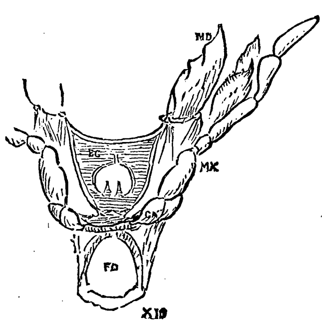


FIG. 6.—Endocranium and maxillary suspensorium of European cockroach (*Periplaneta orientalis*). EC, endocranium; CA, cardo. Other references as in Fig. 5.

A careful examination of the connections in the cockroach, proves, however, that the cardines of the maxillæ are inserted in a ridge which crosses the basis-cranium in front of the occipital foramen (though a slender ridge runs from this part

round the occipital foramen, as usually occurs in insects). This transverse ridge is intimately connected with the roots of the mesocephalic system; and may be deemed a condensed variation of the bee's suspensorium.

The Coleoptera have presented the greatest difficulty here, a difficulty which has been long felt by zoölogists. With the Coleoptera the basi-cranial region is so unlike that of other insects that a special nomenclature has been devised for it; and the terms *mentum*, *submentum* and *gula* are properly confined to the beetles (the application of these terms to other insects has been, in some measure, guess-work). The base of the head failing us as a guide, we started from the other end, or front. Here it was easy to find in the clypeus of Lachnosterna the points from which the mesocephalic pillars ought to descend; and there the pillars actually are, but they appear as involutions of the wall, and they descend not to the vicinity of the occipital foramen, but further forward to the region of the submentum, and near them the maxillary cardines are inserted. The interpretation of these observations is easy. Mr. Huxley has sought the representatives of the beetle's basi-cranial pieces in the neck of the cockroach; the facts now given appear to say that in other insects (as the bee) they are condensed into the very complex and strong system of ridges which borders the front of the occipital opening. The Coleoptera alone have these parts resolved so as to show the primitive arrangement. The fact that they reach the basi-cranium at the point of insertion of the maxillæ, is in complete harmony with what we have seen in the bee. We observed in the basi-occipital region of the head of Lachnosterna, and still more distinctly in the stag-beetle, an overarching frame, enclosing a nervous canal similar to the sternal canal of the thorax. We may, perhaps, detect traces of this in the very intricate cross-bars in advance of the foramen magnum of the bee; so that here the sternal canal and the roots of the mesocephalic and basi-cranial processes are all crowded together. (Thus it is not correct to say that Coleoptera have no endocranium, although Gegenbaur makes a slip when he cites them as an example of largely developed endocranium.)

Only a few words can be added as to the cranial splachnodemes, or that part of the endocranium which consists of hardening of the pharynx. The mouth is floored by a stiff tongue-like plate

(we may call it *lingua*, not to be confounded with the ligule already mentioned). The tip of this lingua is deflected downwards, and from its base run backwards two long barbed processes. Over the mouth is a similar but simpler structure, called epipharynx, and to these the borders of the pharynx are attached, and also muscles. If we force open the mouth (by pulling down the maxillæ), we find the open mouth overarched by epipharynx (connected with the labrum), floored inwardly by the lingua (or inner tongue, formed by the floor of the pharynx), enclosed at the sides by the long tendons of the lingua which are stretched up like faucial door posts. All these hard parts keep open the soft membrane of the pharynx, just as the iron frame of a dredge keeps open the netting attached to it. In the upper part of the cranial cavity are racemose glands which send down a pair of ducts to the inner tongue. The great salivary apparatus of the thorax sends forward its ducts which unite and penetrate through the basi and medi-labium to the ligule or long outer-tongue.[1]

It would be premature, at the present stage of our knowledge, to theorize upon these facts. They indicate a fundamental unity of structure of the heads of all insects; but how far and in what directions it is varied, and what is its relation to other parts of the body, are questions needing further research.

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MYA ARENARIA IN SAN FRANCISCO BAY.

BY ROBERT E. C. STEARNS.

IN November, 1874, Dr. W. Newcomb, who at that time resided in California, described in the Proceedings of the California Academy of Sciences, a species of Mya which had been given to him by the well-known collector, Henry Hemphill, who detected several specimens of the form on the shore of Alameda county, on the eastern side of San Francisco bay.

The specimens were about two-thirds of the usual average size

[1] Siebold discovered a triple salivary system in the bee; but the text books are still sadly at variance with each other and with the facts, in their treatment of this part of the subject. Some place the bee's salivary glands in the head, some in the thorax, and some say they are sometimes in one part and sometimes in the other!